

Insect hibernation on urban green land: a winter-adapted mowing regime as a management tool for insect conservation

Philipp Andreas Unterweger¹, Jorinde Klammer¹, Manuela Unger¹, Oliver Betz¹

¹ *Institut für Evolution und Ökologie, Evolutionsbiologie der Invertebraten, Eberhard Karls Universität Tübingen, Auf der Morgenstelle 28, 72076 Tübingen, Germany*

Corresponding author: Philipp Andreas Unterweger (philipp.unterweger@uni-tuebingen.de)

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Abstract

Insect conservation is challenging on various ecological scales. One largely neglected aspect is the quality of undisturbed hibernation sites. This study aims to fill a lack of knowledge concerning insect hibernation on uncut meadows persisting in urban green spaces during the winter season in a middle-sized town in south Germany. During two years of sampling, 13,511 insect specimens of the orders Heteroptera, Hymenoptera, Coleoptera and Diptera were caught from their winter stands. The specimens were assigned to 120 families and 140 taxonomic species were determined from the orders Heteroptera, Coleoptera and Diptera and 324 morphotypes from the orders Hymenoptera, Coleoptera and Diptera. The data indicate the importance of winter fallows for insect hibernation. Unmown meadows offer additional plant structures in winter (flower heads, stems, tufts and leaves) that are absent from mown ones. This increased structural diversity results in both higher species diversity and numbers of insect individuals during spring emergence. The results of this study thus emphasise the value of unmown structures for insect conservation and suggest a mosaic-like cutting maintenance of meadows, way- and river-sides and other green infrastructure in both the urban area and the open landscape.

Keywords

Coleoptera, Diptera, green space, habitat protection, Heteroptera, hibernation, Hymenoptera, insect decline, meadow, mowing, urban ecology

Introduction

The multifaceted threat and the extent of worldwide and massive insect loss (e.g. Maes and Van Dyck 2001, Thomas et al. 2004, Wenzel et al. 2006, Fonseca 2009, Barnosky et al. 2011, Fattorini 2011, Schuch et al. 2012, Habel et al. 2015) have become an increasingly important factor in the discussion of an expected worldwide mass extinction of species (e.g. Barnosky et al. 2011, Betz 2011, Ceballos et al. 2017). Current studies of flying insects have estimated about 75 % of biomass loss in the last twenty years in some parts of the world (e.g. Potts 2012, Schuch et al. 2012, Sorg et al. 2013, Ollerton et al. 2014, Hallmann et al. 2017). The many reasons for the observed insect decline include (1) the effect of insecticides with a special focus on neonicotinoids (e.g. Biesmeijer et al. 2006, Mason et al. 2013, Ollerton et al. 2014, Godfray et al. 2015), (2) the loss of diverse and small-scale agriculture (e.g. Benton et al. 2002, Robinson and Sutherland 2002), (3) the homogenisation and degradation of ecosystems (e.g. Garcia 1992), (4) increasing landscape urbanisation (e.g. Williams et al. 2009, Fattorini 2011) and (5) habitat fragmentation (e.g. Tilman et al. 2001). At least in the temperate zone, one major impact on insect mortality results from the high frequency of green land mowing in all areas, including agricultural meadows, edges, margins, fallows, waysides, riversides, urban green spaces and private gardens (e.g. Ellenberg and Leuschner 2010, Diacon et al. 2011, Schuch et al. 2012, Schweitzer et al. 2012, Meyer et al. 2013, Buri et al. 2014, Haufe et al. 2015). Under such regimes causing intensive disturbance, many insects are either directly killed or are unable to accomplish their development from the egg to the adult stage. In this regard, intense green land mowing is comparable to the adverse effects of overfishing in aquatic ecosystems from which more individuals (including the larval stages) are removed from the system than can naturally reproduce or migrate.

In Central Europe, natural and anthropogenic grasslands can be seen as hotspots for plants and insects (Hobohm 2000) and contain numerous threatened species (Pärtel et al. 2005). The continuous use of natural hay meadows and pastures has led to the establishment of plant and insect communities especially adapted to this ecosystem (e.g. Humbert et al. 2009). The intensification of grassland maintenance (fertilisation, high mowing intensity, ploughing, drainage) has had a negative influence on the diversity of flowering plants (Meyer et al. 2013), on the animals depending on these resources (Schuch et al. 2012, Haufe et al. 2015) and on several ecosystem functions (Garcia 1992). Every mowing event can kill up to 50 % of the invertebrate fauna of a grassland ecosystem (Diacon et al. 2011), affecting the life on a meadow by (1) the mowing incident itself, (2) the preparation for loading (swathing) and (3) the loading process (Di Giulio et al. 2001, Humbert et al. 2009). Moreover, (4) the change in the microclimate including desiccation (Albrecht et al. 2010) after mowing further contributes to the loss of invertebrate biomass on meadows. Late cutting in concert with the reduction of mowing events and the extraction of nutrients from mown meadows lead to increased plant diversity (Diacon et al. 2011, van de Poel and Zehm 2014). For meadows, several cultivation regimes have been established, i.e. intense *versus* reduced

mowing (Pavlů et al. 2011), mulching (Doležal et al. 2011) or grazing (Fischer and Wipf 2002, Pöyry et al. 2005, Diacon et al. 2011). In a systematic literature review, van de Poel and Zehm (2014) have summarised the literature with regard to the way that various modes of natural green space mowing affect the fauna and have provided suggestions for the mitigation of the adverse effects of mowing on insects and other groups of animals.

In Central Europe, the expansion of urban areas is rapidly increasing. In west Germany, the areas settled by humans have increased by about 140% in the past fifty years (Russell et al. 2005, Kompakt 2011). At present, 13.6% of the area of Germany is covered by settlements and infrastructure (Bundesamt 2011, 2016); such urban areas can provide a wide range of diverse habitats with positive impacts on, for instance, flower-visiting insects (Matteson et al. 2013). This explains the current focus of conservationists on these easily introducible replacement biotopes (Bischoff 1996). If wild bees are taken as an example, half of the endemic species in Germany can be found in urban areas (Westrich 1989); for example, 258 bee species have been recorded in the city of Stuttgart (Schwenninger 1992, Schwenninger 1999). Although urban green spaces cannot provide the same long-term resources, continuity and habitat qualities as natural areas, the protection of urban nature must be considered an important part of biodiversity projects (Müller 2005).

The general positive effect of management reduction in urban grasslands on insect diversity and numbers (including endangered species) has been evaluated in several previous research projects on a diversity of insect groups such as grasshoppers (e.g. Hiller and Betz 2014), true bugs (e.g. Unterweger et al. 2017b), beetles (e.g. Ade et al. 2012), wild bees (e.g. Wastian et al. 2016) and butterflies (e.g. Kricke et al. 2014). These studies argue in favour of a reduced mowing regime (e.g. once to twice a year) to raise and stabilise both insect species diversity and biomass during the growing season. In the research area in Tübingen (south Germany), the above-mentioned studies of Ade et al. (2012), Hiller and Betz (2014), Kricke et al. (2014), Wastian et al. (2016), Unterweger et al. (2017b) that were performed in the framework of the Initiative Bunte Wiese (i.e. “The colourful meadow initiative”) and of Unterweger and Braun (2015, 2017), Unterweger et al. (2015), Unterweger (2017) form the baseline and provide the motivation of this current study.

Research questions

Insect protection measures must be primarily focused on the egg and larval habitat during the entire year. In the present study, previous investigations have been expanded by considering the entire life cycle of an insect (Duelli and Obrist 2003, Tscharntke et al. 2005) with respect to the availability of habitat resources during the winter season. Diacon et al. (2011) advises that 10% of a meadow should be kept unmown as a refuge for fleeing insects after a cutting event. Such refuges can provide shelter for the insect populations to recolonise the disturbed part of the meadow. Brauer (1871) was

probably the first person to mention that winter causes the greatest effect on arthropod populations, since the population size that survives the winter largely determines abundance in summer (Leather et al. 1993). These two aspects, namely protection zones and overwintering spaces, should in the authors' view, be combined to maintain dynamic populations on meadows.

In the present study, the authors focus on urban meadows as hibernation sites for insects. Meadows can be sub-divided into various structural layers (e.g. Benedetter-Herramhof and Bejvl 2009) such as flower, stem and ground layers that play diverse roles for hibernating insects (Frey 1913, Mansingh 1971, Denlinger 2002), especially since adults, larvae and eggs need different environmental conditions. Renken (1956) and Boness (1953) have postulated that insects migrate to more protected areas (e.g. shrubs, trees, deadwood, soil) to reduce the risk of freezing to death. Meadows that remain unmown throughout the winter and that therefore show a high structural diversity of dry herbal and grassy plant structures, may also provide habitats suitable for hibernation (e.g. Schmidt et al. 2008, Rothenwöhrer 2012, Rothenwöhrer et al. 2013).

Focusing on urban public green spaces, the present contribution explores the differences for insect populations between meadows unmown in winter *versus* mown meadows. Second, the significance of various herbal structures (i.e. flower heads, stems, tufts, leaves) of winter plant stands is evaluated. These results are analysed with respect to the collection of ecological data concerning the hibernation sites used by the representatives of various insect orders (i.e. Coleoptera, Heteroptera, Diptera, Hymenoptera), families and species that potentially provide insect-based ecosystem services (e.g. pollination, pest control). To test the effect of hibernation areas, emergence traps (photo-electors) were used in early spring in order to compare the hatching of insects. In particular, the authors focused on (1) the general effect of autumn mowing on the emergence in the following spring, (2) the temporal development of the total insect emergence from the winter stands on a weekly basis over the course of spring and early summer, (3) the evaluation of the value of the various herbal structures for insect hibernation, (4) the role of herbal structures for the hibernation of various insect orders, (5) the extent of insect hibernation within the soil and (6) the importance of stems and flower heads for the hibernation of insect species. These questions are addressed in two experiments, referred to as experiment 1 and 2 in this work.

Material and methods

The data collection for this study was divided into two main experiments that both aimed at analysing the effect of unmown urban green spaces as potential habitats for hibernating insects. Whereas experiment 1 investigated the use of various plant structures (flower heads, stems, tufts, leaves) existing in mown *versus* unmown winter stands of meadows for hibernation, experiment 2 additionally focused on the soil of unmown meadows as a hibernation site for insects. Data collection occurred in 2014 from mid February to mid June, with experiment 1 being repeated in 2015 for verification purposes.

Experimental design and statistical analysis

Square-shaped emergence traps (photo-electors, see Fig. 1) were used with a lateral length of 50 cm and were covered by black insect fabric (mesh size: 2500 meshes cm⁻², monofil-gauze, bioform.de, Nürnberg). A white collecting container (filled with 100% ethylene glycol (C₂H₆O₂)) was placed on top, trapping the light-seeking insects.

The sampling sites (100–1000 m²) were urban meadows in the city of Tübingen, Germany (48°32'15.9"N, 9°2'28.21"E) that had been mown twice a year (end of June and end of September) for at least two years. In both experiments, only one half of each meadow was mown at the end of June (unmown in autumn), whereas the other half was mown at the end of June and the end of September (mown in autumn).

Figure 2 shows the structure and the setup of the two experiments.

Experiment 1 (Fig. 2 blue): This experiment was designed to evaluate (1) the differences between autumnal mown and unmown meadows and (2) the role of different plant structures for insect hibernation. The authors used 48 photo-elector traps (including 10 blind traps) with tissue-sealed bottoms (Fig. 1) to avoid the entrance of animals from the ground. A volume of two litres of plant material per management type and plant compartment was placed into the traps. The eclector traps were randomly scattered on a separate open site made available for this experiment.

Experiment 2 (Fig. 2 red): The setup of this experiment allowed additional information to be attained on insect hibernation in the soil. Twenty four (24) eclector

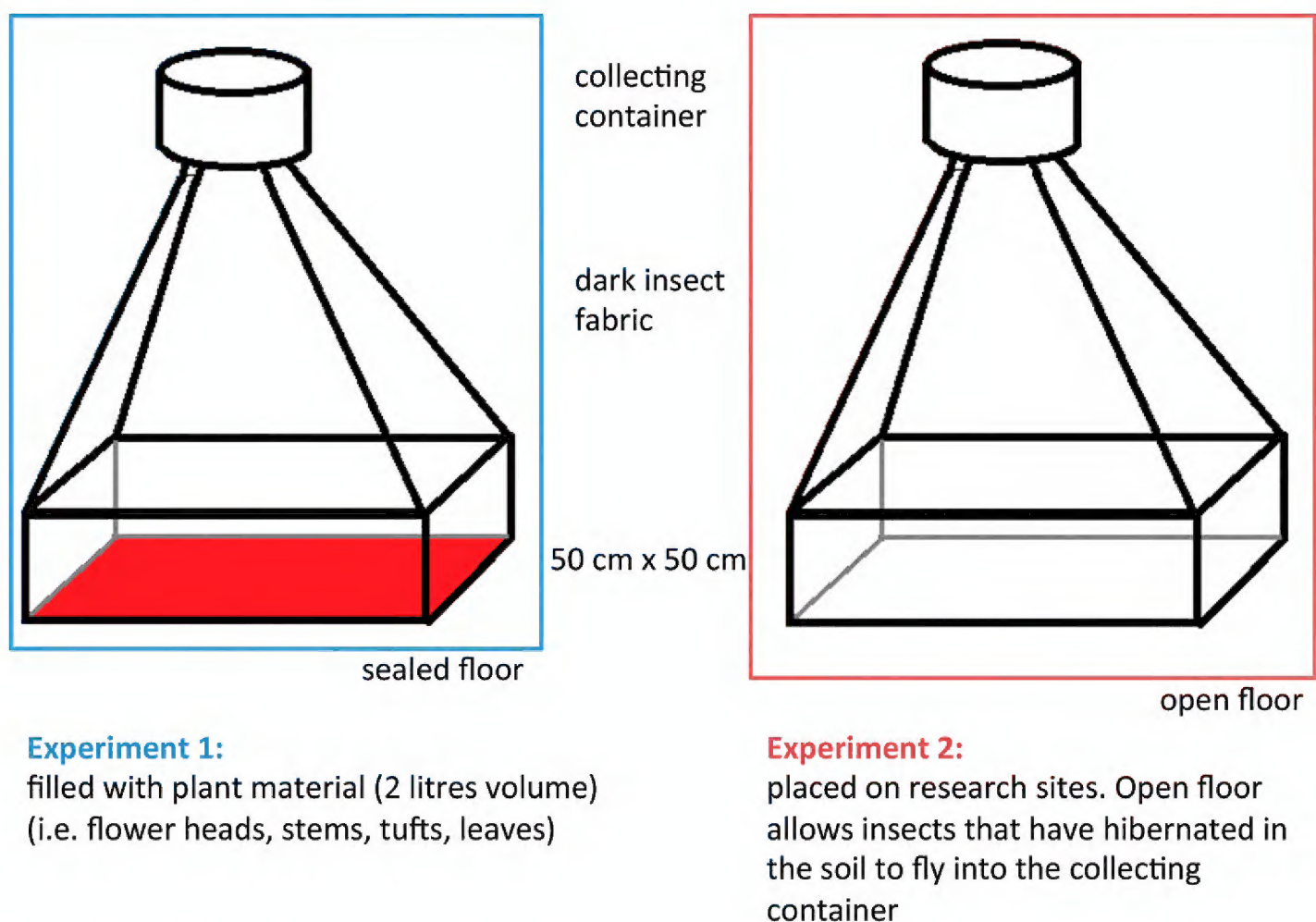


Figure 1. Model of the emergence traps of experiments 1 and 2.

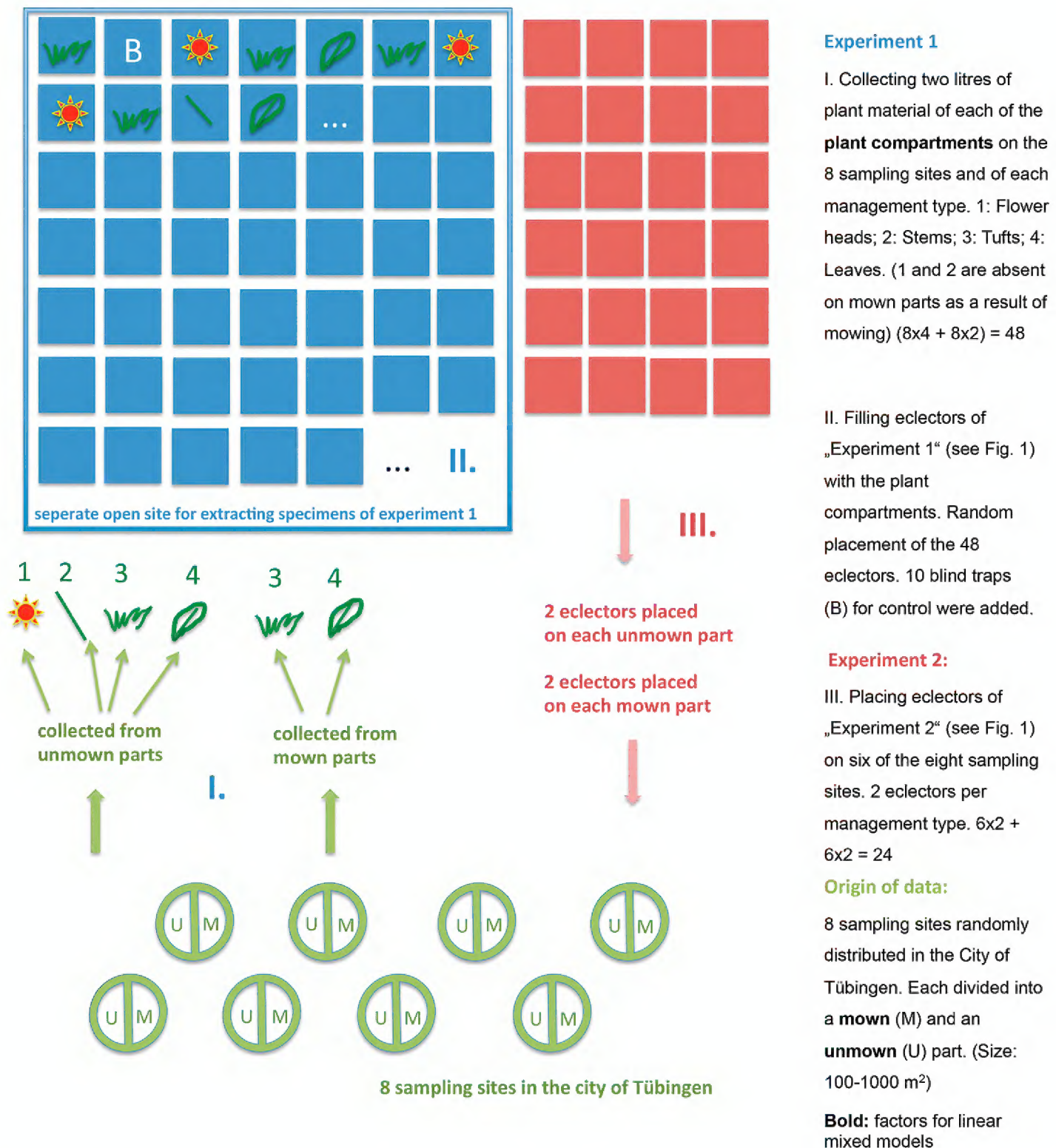


Figure 2. The experimental design for data collection of experiment 1 (blue squares) and experiment 2 (red squares) from eight sampling sites (green circles) divided into a mown (M, mown in autumn) and an unmown (U, without autumn cut) part. Green arrows indicate the collection and sorting of the plant structures. Red arrows indicate the placement of the eclectors on the sampling sites. In experiment 2, only six sampling sites could be used because of vandalism.

traps without sealed bottoms were directly placed (without additional filling with plant material) on six sampling sites (Fig. 1). The sampling sites were subdivided into an autumnal mown and an autumnal unmown part. Two traps per management type were randomly positioned on each sampling site (i.e. two on the mown and two on the unmown part).

In both experiments, the adult insect individuals were collected in the sampling pots every week from February to June. The insects were stored in small twist-top vials in 70 % ethanol for later identification and preparation.

Preparation and identification

True bugs and some large beetles from experiment 1 and all individuals from experiment 2 were pinned, whereas all the other insects were stored in 70% ethanol. The determination of the insect orders was performed based on Schaefer and Bohlken (2000), Bährmann and Müller (2005), Stresemann and Klausnitzer (2011). For the determination of families and species, various determination keys were used (Heteroptera: Stichel (1955, 1958, 1961, 1962), Wagner (1966, 1967), Wachmann (1989, 2006), Hymenoptera (excluding ants): Schmiedeknecht (1907), Goulet and Huber (1993), Coleoptera: Reitter (1908), Freude et al. (1965 ff.), Harde et al. (1981), Hürka (2005), Rheinheimer and Hassler (2010), Diptera: Goulet and Huber (1993), Venn (2004), Oosterbroek (2006), Kotrba and Haldimann (2014)). The orders Collembola, Sternorrhyncha and Lepidoptera and all larvae remained unconsidered. All captured insect specimens were deposited at the insect collection of the University of Tübingen, Morgenstelle 28E, Evolutionary Biology of the Invertebrates.

Levels of identification

In order to consider as many taxonomic groups as possible within an acceptable time period, a frequently used taxonomic shortcut was applied by identifying all taxa only as detailed as required, occasionally termed taxonomic sufficiency (Ellis, 1985) or lowest practical taxonomic level (LPT) (e.g. Hanula et al. 2009, Kutschbach-Brohl et al. 2010). This rapid biodiversity assessment (Oliver and Beattie 1993, 1996a, b) allows non-specialists with basic entomological training to distinguish between standardised (previously defined) groups. The lowest practical taxonomic levels used in this study are shown in Table 1. In some taxonomically difficult groups (some individuals of Hymenoptera, Coleoptera and Diptera), morphotypes were distinguished within the category of the family. Size (i.e. body length) scaling (measured in millimetres and grouped in 0.5-mm clusters) was used to distinguish morphometric groups per family (Daly 1985, Schweiger et al. 2005, Mazón 2016). Ants were not considered as they occurred in too great numbers.

Statistical methods

All statistical analyses were performed with regard to the Shannon index (Mühlenberg 1993), the number of individuals and the number of species/morphotypes with SPSS (IBM, SPSS Statistics 22) and JMP (JMP 13.0). In order to test the influence of both the mowing regime and the plant structures for insect hibernation, linear mixed models (JMP standard settings) were applied with Tukey's HSD post-hoc comparisons. The models were constructed by using means over the sampling sites and by considering the parameters "year" and "weekly sampling date" as random factors. The authors distinguished between eight sampling sites (see Figure 2) in experiment 1 and six by combining experiments 1 and 2 (as only six of these sampling sites were used in both the experiments).

Table 1. Levels of identification within each insect order considered in this study.

Insect order	Level of identification
Heteroptera	Species level (confirmed by Dr. Christian Rieger, Nürtingen)
Hymenoptera (excluding ants)	Family level, all individuals of the various families were measured and these groups were counted as morphotypes
Coleoptera	Species level if scientifically confirmed by external expert (Dr. Nadein (Tübingen) for Chrysomelidae, Dr. Salamon (Hannover) for Staphylinidae). Otherwise determination at lowest practical taxonomic level (LPT). These determinations (species level, genus, family) were counted as morphospecies
Diptera	Family level; all individuals of the various families were measured and these groups were counted as morphotypes; the scientific validation of the families by Dr. Sabine Prescher (Braunschweig), Dr. Anke Schäfer (Weitramsdorf) and Gerrit Öhm (Wasserhausen) led to some lower level identifications (genus, species)

The comparisons between the insect eclosion abundances per square metre in the spring of unmown *versus* mown meadows (in experiment 1) were made with a Wilcoxon test by using SPSS. Results up to a significance level of 0.05 ($p < 0.05$) were categorised as significant. A trend towards significance was accepted up to a significance level of 0.1 ($p < 0.1$).

Results

In the two years of sampling, a total sum of 13,511 insects of the orders Heteroptera, Hymenoptera, Coleoptera and Diptera were sampled in both experiments. The authors identified 120 families, 140 taxonomic species and 324 morphotypes (see Suppl. material 1 of the electronic appendix).

Overall distribution of individuals, families, species and morphotypes in both the experiments (experiments 1 and 2 pooled)

Table 2 presents the total occurrence of insects in the two experiments subdivided into the categories of families, species and morphotypes. Mown (with autumn cut) and unmown meadows (without autumn cut) and the various plant compartments are also distinguished.

Evaluation of autumn mowing effect for spring emergence (experiments 1 and 2 pooled)

One of the major interests was the evaluation of the influence of the mowing regime on insect hibernation in the investigated meadows. Therefore, the means between autumnal mown *versus* unmown meadows were compared. The comparison was performed with regard to the Shannon index ($p < 0.001$), the number of individuals ($p < 0.001$) and the number of species including morphotypes ($p = 0.60$) (Figure 3).

Table 2. Total numbers of individuals (I), families (F), the validated taxonomic species (S) and the morphotypes (T) itemised by insect order over both the pooled experiments. Counts are divided into mown *versus* unmown sites and into the various plant compartments (organs, Experiment 1 only) flower heads, stems, tufts, leaves. “–” = not applicable. A detailed list of the sampled species is provided in the electronic supplement (Suppl. material 1).

	Heteroptera				Hymenoptera				Coleoptera				Diptera			
<i>families</i>	10				38				37				35			
<i>species / types</i>	34 / –				– / 135				68 / 141				38 / 48			
	<i>I</i>	<i>F</i>	<i>S</i>	<i>T</i>	<i>I</i>	<i>F</i>	<i>S</i>	<i>T</i>	<i>I</i>	<i>F</i>	<i>S</i>	<i>T</i>	<i>I</i>	<i>F</i>	<i>S</i>	<i>T</i>
<i>unmown</i>	78	9	27	–	2221	28	–	118	730	32	60	107	5723	35	33	43
<i>mown</i>	12	5	9	–	869	20	–	82	420	31	30	87	3458	30	16	35
<i>flower heads unmown</i>	10	3	4	–	579	18	–	53	76	17	17	27	579	15	6	18
<i>flower heads mown</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>stems unmown</i>	7	3	5	–	230	12	–	40	102	16	17	31	370	14	5	17
<i>stems mown</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>tuft unmown</i>	9	5	6	–	274	14	–	47	174	17	27	41	792	20	8	21
<i>tuft mown</i>	3	2	3	–	184	13	–	42	86	20	15	34	717	23	6	21
<i>leaves unmown</i>	4	2	2	–	419	18	–	62	85	16	18	29	687	22	11	24
<i>leaves mown</i>	2	2	2	–	140	11	–	23	79	16	19	25	464	16	3	20

Time course of springtime insect eclosion (experiments 1 and 2)

The insect emergence from the middle of February to the middle of June of the individuals of the various insect orders is summarised in Figure 4. Insect eclosion varies over time and within the studied insect orders.

Plant compartments as resources for insect hibernation in consideration of autumnal mowing (experiment 1)

In contrast with the unmown meadows, flower heads and stems were absent on the meadows with an autumn cut (see Table 2: “–” = not applicable), so that these resources were not available to insects during the winter.

The following results are based on the linear mixed model analyses (Fig. 5) and only describe significant results.

Shannon index: The highest Shannon index values were found in tufts with no mowing in autumn. Flower heads were used less for hibernation compared with the other plant compartments.

Number of individuals: The number of individuals shows, in comparison with the plant compartments, the fewest numbers in stems (absent in mown meadows) and in the structures of the mown areas.

Number of species/morphotypes: On unmown meadows, the species/morphotype comparison did not show any significant differences between the plant compartments. The differences between the compartments of mown *versus* unmown areas are significant for tufts and leaves. The important fact that flower heads and stems are missing as hibernation spaces on mown areas stresses the ecological value of these plant compartments on unmown meadows.

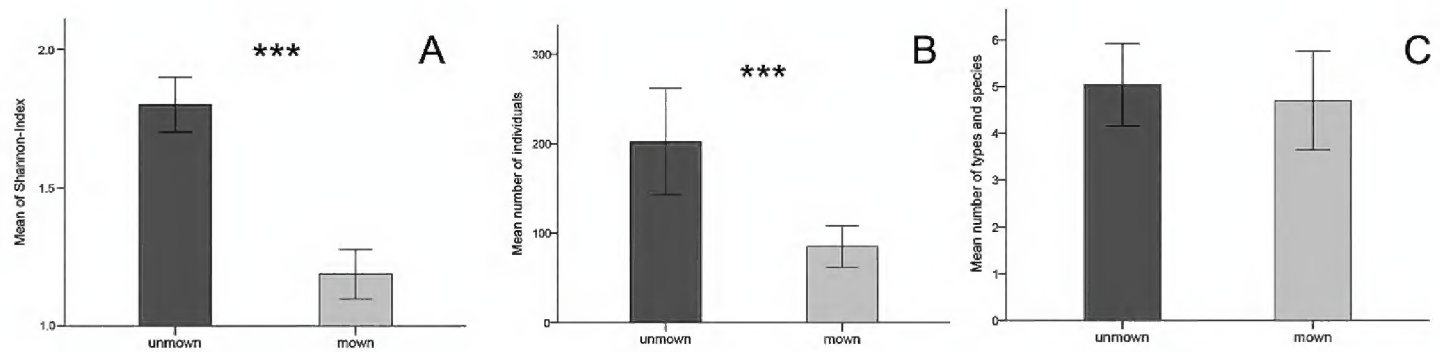


Figure 3. Impact of autumn mowing on the arithmetic mean (\pm 95 % CI) of **A** Shannon index **B** the number of individuals and **C** the number of species/types. Asterisks indicate significant effects of the factor mowing regime as derived from linear mixed models (* $p < 0.05$; ** $p < 0.005$; *** $p < 0.001$). Shannon: $p < 0.001$, DF: 1,392, F-ratio: 121.8; Number of individuals: $p < 0.001$, DF: 1,55, F-ratio: 21.9; number of species/morphotypes: $p = 0.60$, DF: 1,56, F-ratio: 0.2651 ($n = 6$).

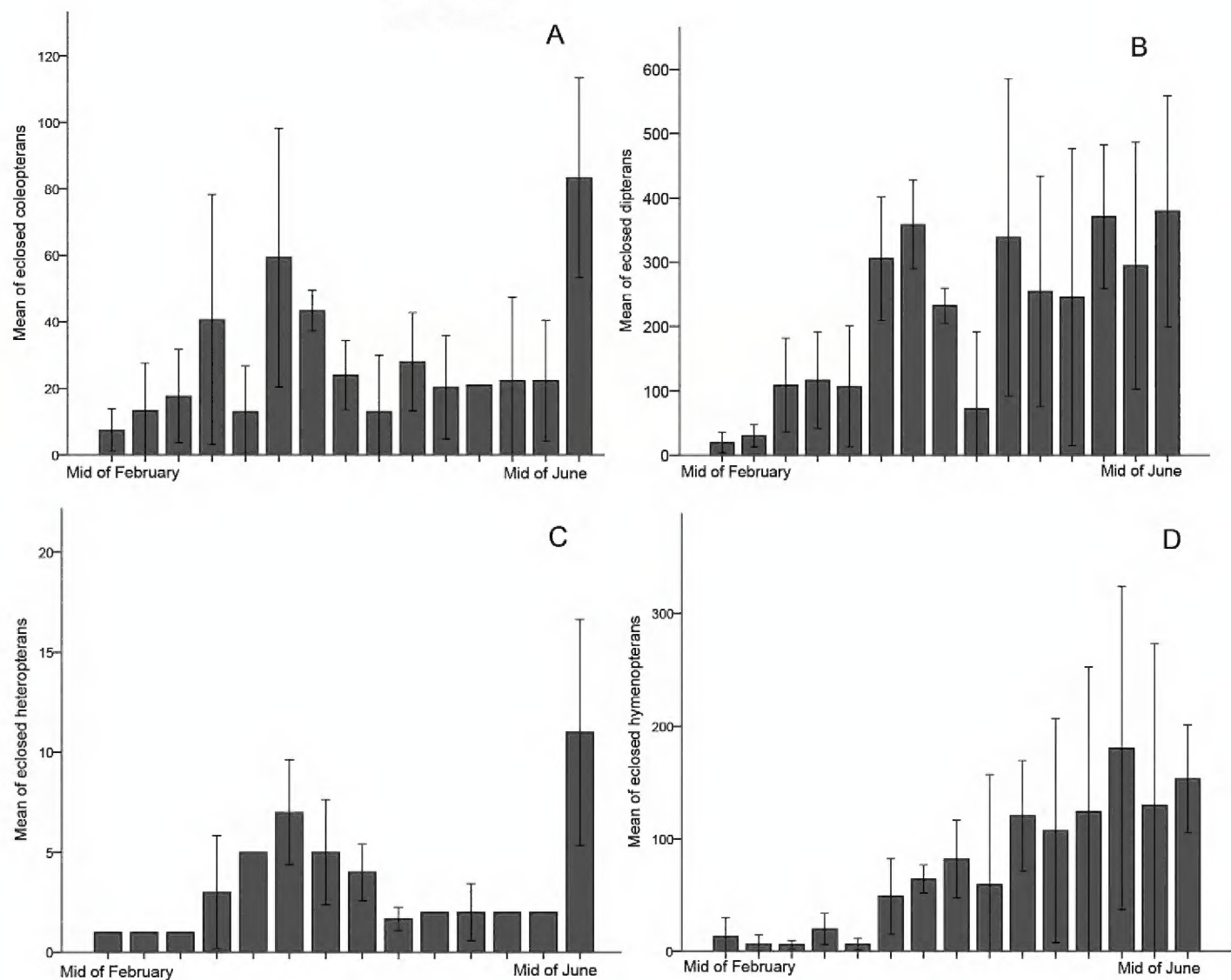


Figure 4. Temporal development of weekly insect emergence in spring and early summer. The mean (\pm SD) of all captured individuals per order that hatched from the pooled experiments 1 and 2 were counted ($n = 8$).

Comparison of the various insect orders and their hibernal occurrence in plant organs (experiment 1)

To test the hypothesis that, in the studied insect orders, special preferences occur regarding hibernation in the various plant compartments, linear mixed models were

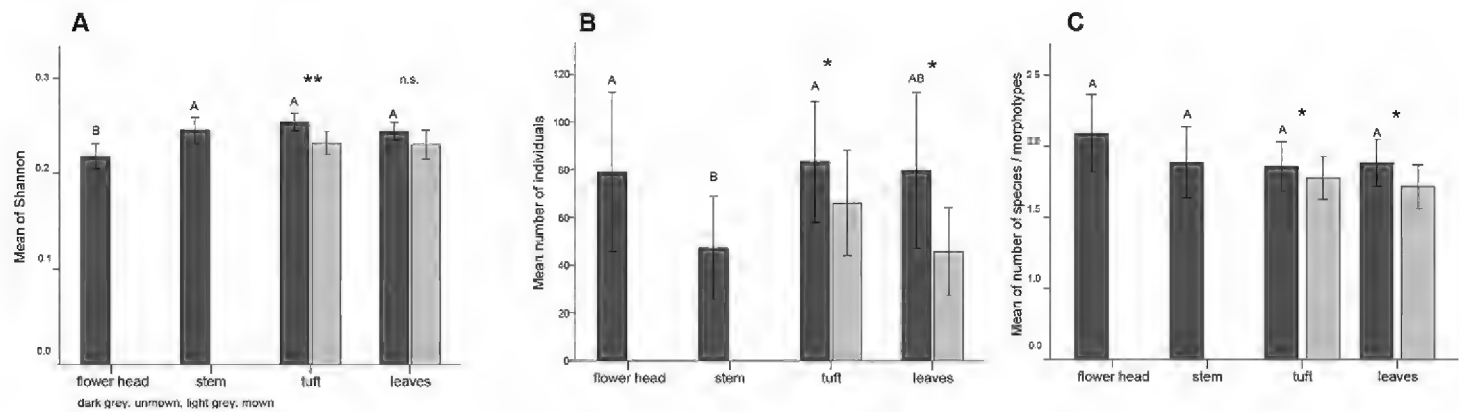


Figure 5. Significance of plant compartments as insect hibernation sites with respect to the arithmetic mean (\pm 95 % CI) of **A** the Shannon index **B** number of individuals and **C** number of species / morphotypes subdivided by mowing regime. Flower heads and stems are not found on mown meadows. Different capital letters indicate pairwise significant differences between plant compartments of unmown (dark grey) sampling sites, whereas asterisks indicate significant differences (* $p < 0.05$; ** $p < 0.005$; *** $p < 0.001$) between both the mowing regimes based on Tukey's HSD post-hoc comparisons after linear mixed models. Shannon index (only significant results reported): $p < 0.001$; DF: 3,5; F-ratio: 8.3 (flower head – stem: $p < 0.005$, flower head – tuft: $p < 0.001$, flower head – leaves: $p < 0.005$). Unmown – mown testing: tuft: $p < 0.005$; DF: 1,873; F-ratio: 8.8. Number of Individuals (only significant results reported): $p < 0.001$; DF: 1,97; F-ratio: 4.1 (flower head – stem: $p < 0.05$, stem – tuft: $p < 0.05$). Unmown – mown testing: tuft: $p < 0.05$; DF: 1,301; F-ratio: 4.0. Leaves: $p < 0.05$; DF: 1,20; F-ratio: 5.0. Species/morphotypes: $p < 0.05$; DF: 1,93; F-ratio: 1.6. Unmown – mown testing: tuft: $p < 0.05$; DF: 1,303; F-ratio: 4.0. Leaves: $p < 0.05$; DF: 1,20; F-ratio: 5.0. $n = 8$.

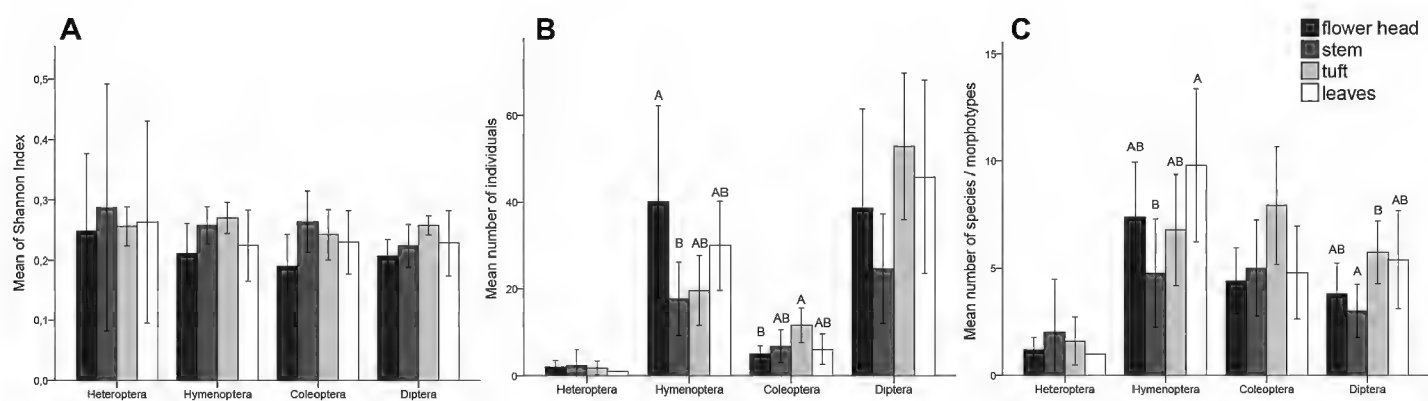


Figure 6. The distribution of the insect orders with respect to arithmetic mean (\pm 95 % CI) on the various plant organs showed no significant differences with respect to the Shannon index (**A**). The number of individuals (**B**) is distributed across the plant compartments with no significant trend in the orders of Heteroptera and Diptera, whereas a strong tendency to significance can be seen in some hibernation places of Hymenoptera (linear mixed model $p < 0.05$; DF: 3,4; F-ratio: 2.8; flower head – stem: $p = 0.065$; flower head – tuft: $p = 0.095$). Significantly more coleopterans hibernate in tufts compared with flower heads (linear mixed model $p < 0.05$; DF: 3,376; F-ratio: 3.5; flower head – tuft: $p < 0.05$, tuft – leaves: $p = 0.074$). The number of species (**C**) was not significantly different across plant compartments for Heteroptera and Coleoptera. For Hymenoptera, significantly more species occurred in leaves compared with stems (linear mixed model $p = 0.075$; DF: 3,173; F-ratio: 2.4; leaves – stem: $p < 0.05$). For Diptera, a strong trend showed that more individuals hibernated in tufts compared with stems (linear mixed model $p < 0.05$; DF: 3,76; F-ratio: 2.8; stem – tuft: $p = 0.072$). Significant differences between the plant compartments within each insect order, as based on Tukey's HSD post-hoc comparisons after linear mixed models, are indicated by different capital letters ($n = 8$).

applied to the data from the unmown meadows that showed all plant compartments (Fig. 6).

The Shannon index did not show any significant patterns (Fig. 6A).

Number of individuals: By trend, significantly more hymenopterans hibernated in flower heads compared with stems and tufts. Coleopterans preferred tufts significantly more than flower heads with an additional trend to significance between tufts and leaves.

Number of species/morphotypes: The highest species/morphotype number of Hymenoptera can be found in leaves and tufts for Diptera.

Insect hibernation in the soil (experiments 1 and 2)

To investigate the importance of soil for insect hibernation, the species lists were compared with respect to the single occurrence of the species in experiment 2 (Table 3). The individuals of species that occurred in experiment 2 only (and not in experiment 1) were presumed to have hibernated in the soil (brown-labelled in Suppl. material 1, electronic supplement), because the eclectors used in this experiment had open bottoms, whereas the eclector bottoms used in experiment 1 were sealed (Fig. 1).

Importance of stems and flower heads for insect hibernation (experiment 1)

The results of experiment 1 were used to evaluate the importance of flower heads and stems as hibernation sites for insects. Species that only occurred in flower heads and stems are listed in Table 4.

Discussion

The present contribution aims to provide new data for optimising green space management for insect hibernation. Although this study has been performed on public urban green spaces, its results are also relevant for rural grassland. In the cultural landscape, such structures are usually present on waysides, field margins, river slopes, meadow orchards and fallows but not on intensive meadows, because these are usually mown until autumn. These structures are threatened in Europe by intense mowing (e.g. Unterweger and Unterweger 1989, Diacon et al. 2011). In these experiments, the authors tried to consider hibernating species from a variety of insect orders and did not focus on keystone species or species with a special environmental status during the growing season. The focus on pollinators (e.g. wild bees) in insect conservation discussions often neglects other important ecological groups such as predators, parasitoids, decomposers and herbivores. These results allow conclusions to be drawn concerning the ecological / conservation value of meadows left unmown during the autumn for insects in general and for biodiversity by providing useful hibernation sites.

Table 3. Species that are presumed to have hibernated in the soil (see Fig. 1). Only species with confirmation by a taxonomic expert are listed (see Suppl. material 1, supplement: brown species).

Order	Family	Species
HETEROPTERA	Cymidae	<i>Cymus glandicolor</i>
	Lygaeidae	<i>Beosus maritimus</i>
		<i>Drymus ryeii</i>
		<i>Rhyparochromus pini</i>
		<i>Scolopostethus thomsoni</i>
	Miridae	<i>Capsus ater</i>
		<i>Dicyphus annulatus</i>
		<i>Plagiognathus arbustorum</i>
		<i>Plagiognathus</i> cf. <i>chrysanthemi</i>
		<i>Podops inunctus</i>
		<i>Stenodema calcarata</i>
	Nabidae	<i>Nabis ferus</i>
		<i>Nabis rugosus</i>
	Pentatomidae	<i>Palomena prasina</i>
	Rhyparochromidae	<i>Megalonotus emarginatus</i>
	Tingidae	<i>Dictyla humuli</i>
COLEOPTERA	Chrysomelidae	<i>Cassida vibex</i>
		<i>Galeruca tanaceti</i>
		<i>Oulema erichsonii</i>
	Staphylinidae	<i>Philonthus carbonarius</i>
		<i>Quedius boops</i>
		<i>Quedius curtipennis</i>
		<i>Quedius maurus</i>
		<i>Quedius nitipennis</i>
		<i>Scopaeus minutus</i>
		<i>Staphylinus dimidiaticornis</i>
DIPTERA	Opomyzidae	<i>Geomyza tripunctata</i>
		<i>Geomyza venusta</i>
		<i>Opomyza florum</i>
		<i>Opomyza germinationes</i>
	Stratiomyiidae	<i>Beris geniculata</i>
		<i>Chloromyia formosa</i>
	Syrphidae	<i>Dasysyrphus albostriatus</i>
		<i>Platycheirus</i> cf. <i>scutatus</i>
		<i>Syrphus ribesii</i>
		<i>Syrphus torvus</i>
	Tephritidae	<i>Chaetorellia stylata</i>

Insect hibernation – the impact of autumnal mowing

These results show that meadows without autumn cut offer a huge potential for hibernating insects. The value of unmaintained structures (e.g. field margins) for the number of both species and individuals of animals has been demonstrated in numerous studies (e.g. Lys and Nentwig 1992, Thomas et al. 1992a, Hawthorne et al. 1998, Fournier and Loreau 1999, Pfiffner and Luka 2000, Wiedemeier and Duelli

Table 4. Species that only occurred in flower heads and stems. Only species with confirmation by a taxonomic expert are listed (see Suppl. material 1, electronic supplement: green species).

Order	Family	Species	Flower head	Stem
HETEROPTERA	Anthocoridae	<i>Cardiastethus fasciiventris</i>	2	–
	Lygaeidae	<i>Peritrechus geniculatus</i>	1	1
		<i>Scolopostethus affinis</i>	–	2
	Nabidae	<i>Himacerus mirmicoides</i>	1	–
		<i>Nabis brevis</i>	–	1
	Rhyparochromidae	<i>Megalonotus antennatus</i>	–	1
COLEOPTERA	Chrysomelidae	<i>Hispella atra</i>	1	–
		<i>Oulema melanopus</i>	1	–
		<i>Psylliodes napi</i>	1	–
	Staphylinidae	<i>Sepedophilus testaceus</i>	–	1
		<i>Rugilus rufipes</i>	–	1
		<i>Scopaeus gracilis</i>	–	1
		<i>Lathrobium dilutum</i>	–	1
DIPTERA	Tephritidae	<i>Chaetorellia cylindrica</i>	1	–
		<i>Chaetorellia jaceae</i>	14	–

2000, Fournier and Loreau 2001, Peter et al. 2001, Maudsley et al. 2002, Pywell et al. 2005, Saska 2007, Schmidt et al. 2008, Geiger et al. 2009, Anjum-Zubair et al. 2010, Roume et al. 2011). From the standpoint of the entire life cycle of an insect (Duelli and Obrist 2003, Tscharntke et al. 2005), the role of uncut grassland should not be underestimated. These results confirm the high quality of shelter that autumnally unmown meadows offer to insects compared with mown meadows. Autumnal mowing is usually applied in agricultural grassland cultivation to attain additional harvest, to prevent felting (Unterweger and Unterweger 1989) and infestation or simply due to aesthetic aspects (Unterweger et al. 2015) on margins, waysides and other green spaces.

Springtime insect eclosion – the effect of autumnal mowing

This study has revealed higher insect hatchings from autumnal unmown meadows (Fig. 3) and shows a steady rise in the mean number of hatching individuals during the spring season (Fig. 4), whereby interruptions in between are presumably linked to the weather conditions and colder temperatures during May. According to recent studies, the production of insect biomass has rapidly declined during the past decades, at least in Central Europe (Sorg et al. 2013, Hallmann et al. 2017). The authors’ data indicate that a change in green space management and, by extrapolation, the enlargement of unmown hibernation fallows, waysides and other stripes, could result in an increase in the insect populations in the following year. This shows the enormous productivity of unmown meadows and their important role in meeting the food demands of insect-linked predators (such as nesting birds during breeding time). For example, von der

Dunk and Brünner (2016) calculated the requirements for insect food in common swifts (*Apus apus*), which need about 2000 insects per day when nesting. This larger number of insects is part of the various ecological functions of insects and reveals the importance of the functions of the ecosystem.

Soil eclosing insects – the role of soil for hibernation

The comparison of these two experiments allows the authors to discriminate insect species that hibernate in the soil from those using the vegetation further above the ground. In experiment 2, it has been shown that 134 species/morphotypes (254 individuals) can only be found in the soil, whereas 338 species/morphotypes (3530 individuals) use hibernation sites in the vegetation such as flower heads, stems, tufts and leaves (see Tables 2, 3, 4; Suppl. material 1 in the electronic supplement). These data emphasise the significance of the aboveground hibernation sites of meadows. Dunger (1983) distinguished between insects that spend their whole life cycle underground and those that only stay there during parts of their lives. Some Heteroptera, Coleoptera, Diptera and several species of other insect orders tend to use the soil as egg deposition sites (Frost 1959), larval hibernation and development (Dunger 1983). These early stages emerge from the soil in spring and predators were found in the photo-electrodes of experiment 2. The large number of soil specialists (Kühnelt 1950) makes it necessary for many groups of insects to hibernate above the ground. Thus, plant structures also play an important role for hibernation as is supported by these results.

Plant compartments as places for insect hibernation – the role of structural diversity

The structural diversity of the vegetation (including the various plant organs) can largely influence insect diversity (e.g. Otto and Rezbanyai-Reser 1996, Di Giulio et al. 2001). Comparing four plant compartments, it was found that the Shannon index of stems, tufts and leaves was higher compared with that of flower heads (Fig. 5). Rothenwöhrer et al. (2013) noticed the value of meadow structures, especially for stem-boring insects such as species of the family of Cecidomyiidae and the value of long-structured meadows for their protection. Pywell et al. (2005) and Lang (1983) focused on tufts when regarding hibernation on grassland. In stems, the number of hatching individuals was lower compared with that of the other plant compartments, whereas the species richness was similar amongst them. Norton et al. (2014) showed that grass as ground-cover contained the highest abundance of arthropods (excluding Collembola) compared with other ground coverings (leaf litter, bare ground, woodchips). The general importance of this vegetative ground cover is supported by the authors' results, as leaves and tufts play an important role for hibernation (see Fig. 5). In addition to the value of vegetative ground cover, it must be considered that flower heads and stems are totally absent on meadows mown late in autumn (see also: Rothenwöhrer 2012, Rothenwöhrer et al.

2013). In this study, it was found that several insect species (morphotypes not included) require stems and flower heads for hibernation (Table 4 and Suppl. material 1, electronic supplement: green-labelled species). The impact of autumnal mowing causes the total loss of a complete group of insects. This is emphasised in this study by the high number of individuals (1953 individuals, Table 2) that hatched from these compartments on unmown meadows, even if they are not significantly higher compared with those from tufts and leaves. The loss of individuals and shelter (Cattin et al. 2003) is the worst-case scenario for overwintering and recolonisation in spring, whereby the loss of structural diversity caused by the autumnal mowing process reduces the winter protection effect of the meadow (e.g. Potts 2012, Wagner et al. 2014), so that the number of species and individuals decreases, even in the remaining structures.

Insect orders - their hibernal occurrence in plant organs

With regard to the Shannon index, the four analysed insect orders showed a homogeneous distribution across the four plant compartments, i.e. no significant predominance of one order or even differences between the organs were detected (Fig. 6A).

However, in terms of numbers of individuals and species/morphospecies of the various insect orders, differences were found between plant compartments as overwintering sites (Fig. 6B, C).

Heteroptera: Only a few heteropterans hibernated as adults and so their numbers were low until the adults of the egg hibernating species emerged in late June (Boness 1953). This is supported by the low number of adult heteropterans found in this study.

Hymenoptera: For Hymenoptera (mainly parasitoid families of Braconidae and Ichneumonidae), the distribution of individuals amongst the plant compartments shows that they prefer flower heads and leaves compared with stems and tufts for hibernation (Fig. 6). This supports the role of retaining flower heads in winter to provide a reservoir for beneficial insects such as parasitoid hymenopterans (e.g. Albrecht et al. 2010). This finding is further underlined by the dense correlation between the numbers of hymenopterans and dipterans in Figure 6 possibly reflecting a parasitoid-host relationship (Schmiedeknecht 1907, Goulet and Huber 1993). With respect to the species number, the highest hymenopteran diversity occurred in leaves. For agricultural fallows, Bürki and Pfiffner (2000) differentiated the plant compartments with regard to the occurrence of beneficial and pest insect organisms.

Coleoptera: Many beetles prefer tufts for hibernation, a finding that can possibly be explained by their preference for walking instead of flying (Wiedemeier and Duelli 2000). In addition, Pywell et al. (2005), who stress the value of tufts for beetles and spiders, Freude et al. (1965), Boness (1953), Thomas et al. (1992b) and Bürki and Pfiffner (2000) mention a variety of hibernation sites for Coleoptera, such as tufts, stems (reed) and leaf litter.

Diptera: According to this study, tufts form attractive hibernation places for dipterans. In the present investigation (Table 2, Figure 6B), flies tend to be the largest

group on meadows with a focus on plant compartments near the ground, a finding which agrees with the results of Boness (1953). The high value of vegetation compartments for dipterans has previously been discussed by Braune (1971), Bockwinkel (1988) and Schäfer (1993). They postulate that mowing destroys the places in which eggs are deposited and therefore has an enormous impact on insect egg survival. Insect hibernating as adults are in general less affected by mowing, since they are mobile and may be better able to avoid the risks of mowing (Schäfer 1993).

Unmown meadows – their overall role in the ecosystem

Natural meadows with dead winter vegetation and its complex vertical structure have become a rare and endangered biotope in Central European landscapes (Finck et al. 2017). The loss of adequate insect hibernating sites (Welling et al. 1987) consequently leads to higher winter mortalities and, in the long term, to a loss of biodiversity. In addition to insects, birds benefit from meadows that are unmown in autumn. Finches (Fringillidae), sparrows (Passeridae), common linnets (*Linaria cannabina*), European goldfinches (*Carduelis carduelis*) and yellowhammers (*Emberiza citrinella*) have been found in Europe on unmown wasteland and margins in high numbers (Wagner et al. 2014). Vickery et al. (1998) and Buckingham et al. (1999) have shown that North American buntings prefer unmown field margins compared with mown fields. The large amount of seeds and hibernating insects and spiders of these structures may be major factors (Moorcroft et al. 2002) attracting birds to unmown land. In general, meadows, slopes and margins are not only mown during the summer, but also in autumn in “preparation for the winter” (urban green spaces and private gardens are also mown in order to tidy up their winter vegetation) (Wagner et al. 2014). However, such management measures may destroy structures essential for overwintering foraging birds, small game and insects hibernating in the vegetation (e.g. Potts 2012, Wagner et al. 2014).

Recommendation for practice

In the following, practical recommendations that follow from the results of these studies are provided.

Adapted mowing concept to stabilise and expand insect populations on grassland ecosystems

The results of this study in combination with the authors’ previous results (Ade et al. 2012, Hiller and Betz 2014, Kricke et al. 2014, Wastian et al. 2016, Unterweger et al. 2017b) suggest an adapted management regime under additional considerations

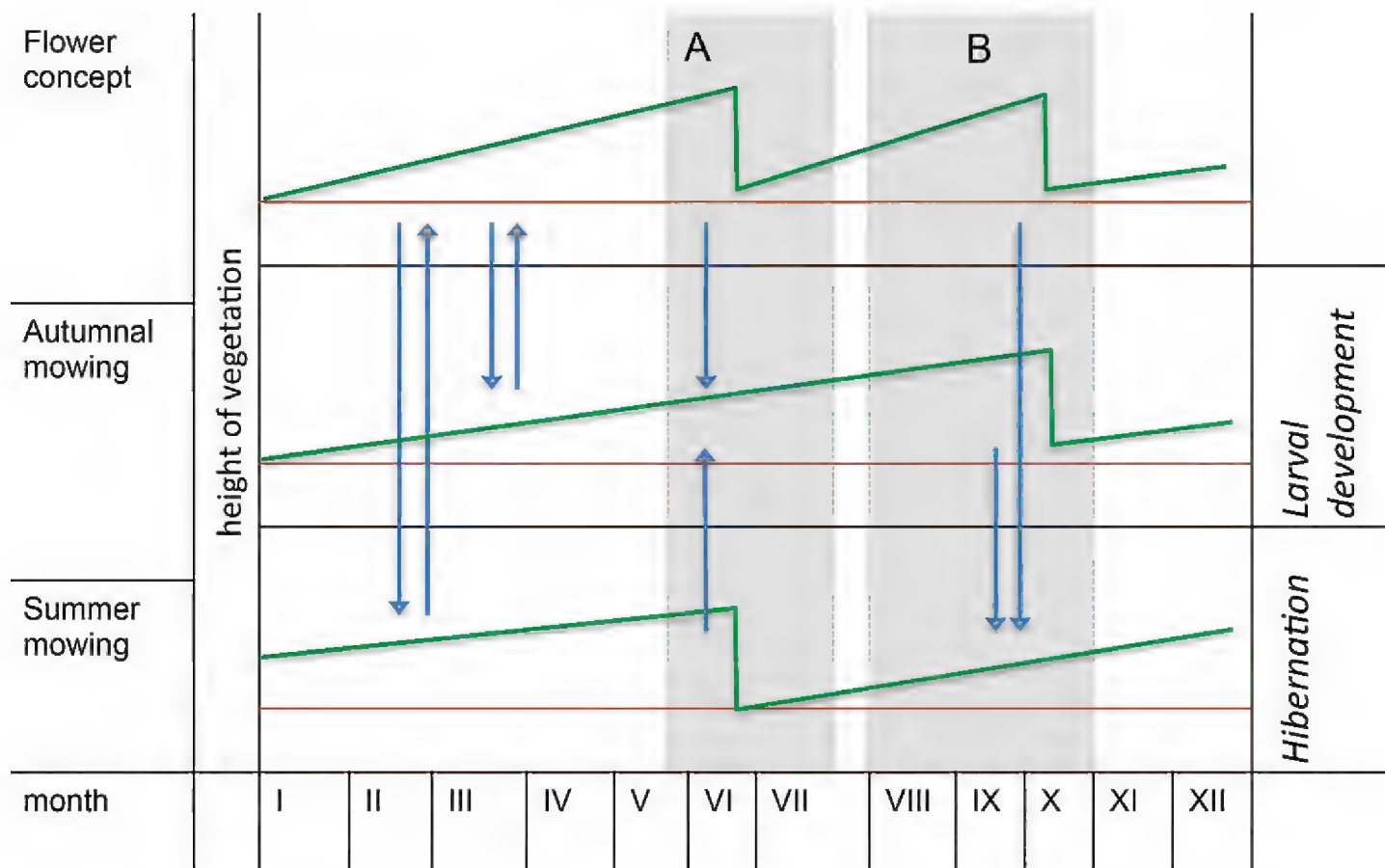


Figure 7. Scheme of an optimised management plan in consideration of the previous entomological studies and the present results. The authors distinguish between three mowing concepts, (1) the “flower concept” for optimising flower diversity and nutrient balance, (2) “autumnal mowing” for reproduction and larval development of late summer insects and (3) “summer mowing” for providing hibernation areas. The green line symbolises a possible course of vegetation height. A and B symbolise mowing periods rather than set mowing dates. The heights of mowing vary randomly (relation to constant (brown) soil baseline) to provide ecologically different situations (from open soil to longer vegetation as hiding places during mowing). The vegetation height of the “summer mowing” starts at a higher level in spring as a result of the vegetation that has remained on the site during winter. Blue arrows show the possible fluctuation between source and sink habitats and the metapopulations in the mosaic mowing system. In all three regimes, the disposal of the cut hay is recommended to avoid overfertilisation and grass dominance.

of sink and source dynamics (e.g. Pulliam 1988, Howe et al. 1991, Watkinson and Sutherland 1995) and metapopulation models (e.g. Harrison 1991, Stelter et al. 1997, Hanski 2004).

The studies of these previous experimental setups (Ade et al. 2012, Hiller and Betz 2014, Kricke et al. 2014, Wastian et al. 2016, Unterweger et al. 2017b) underline the ecological value of management reduction for insect biodiversity. These studies have revealed significantly higher numbers of species and individuals on meadows cut twice a year in combination with the removal of the biomass compared with lawns cut monthly. A mowing regime with two cuts a year (“flower concept” in Fig. 7) also leads to a higher number of dicotyledonous plant species and thus to an increase of flower-visiting insects (Noordijk et al. 2009, Noordijk et al. 2010) and a higher biodiversity on several other levels (e.g. birds, ecosystem functions). In order to take into account the various life cycles of insects, prolonged mowing periods (including the shift be-

tween one and two cuts per year) should be performed rather than mowing large areas at the same time (Humbert et al. 2009).

Even if, in some cases, a once a year mowing regime seems to be too intensive (Dennys and Tschardt 2002, van Buskirk and Willi 2004), this proposed mowing mosaic concept (Fig. 7) helps to reconcile various ecological functions (i.e. reducing nutrient input, raising flower diversity, supporting metapopulation dynamics, stopping succession) and aesthetic and social needs (flower richness, scenic beauty) (Unterwiesing et al. 2017a, Unterwiesing et al. 2017c).

The resulting different types of meadows support insects by allowing them to escape, migrate and find suitable habitats at anytime of the year (Di Giulio et al. 2001, Noordijk et al. 2010). Following the life cycle, especially of grasshoppers or some true bugs (Boness 1953), the “autumnal mowing” regime might be best suited to support their undisturbed larval development from spring to late summer. This concept generally protects insects with late imaginal stages (Boness 1953). The results of the current study especially argue in favour of the “summer mowing” concept (Fig. 7) which provides high quality insect hibernation habitats that can be additionally exploited by winter birds.

The combination of the “flower concept”, the “autumn mowing” and the “summer mowing” and the occurrence of elongated periods during which mowing is possible, instead of the specification of fixed mowing dates, supports metapopulation dynamics and the recolonisation of mown meadows (cf. blue arrows in Fig. 7 symbolising migrations). Thus, the total biomass as a feeding resource, place for reproduction and (winter) shelter is never missing and mobile stages of insects can migrate between these areas. Stepping stones and corridors are beneficial in improving these dynamic mosaics (Valkó et al. 2012). Mosaic-like mowing (Schmidt et al. 2008) should also be considered on more isolated green spaces, as many insects do not move long distances (Sárospataki et al. 2009).

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Supplementary material I

Table with all captured species / morphotypes sorted by order, family and species / morphotype.

Authors: Philipp Andreas Unterweger, Jorinde Klammer, Manuela Unger, Oliver Betz

Data type: species data

Explanation note: Collection: University of Tübingen, Evolutionary Biology of Invertebrates, Auf der Morgenstelle 28, 72076 Tübingen, Germany. Individuals with scientific species name that were checked by a taxonomic expert were counted as taxonomic species (s); all the other determinations were counted as morphotypes (m). Morphotypes are defined by the lowest practical taxonomic level (e.g. Hanula et al. 2009; Kutschbach-Brohl et al. 2010). In some cases, the family or the morphometric body length (in mm, numbers in column C, Mini: smaller than 1 mm) was counted as a morphotype (Daly 1985). In cases for which the determination was not validated by a taxonomic expert, our species determination was checked for plausibility in terms of its geographical occurrence via the Entomofauna Germanica (<http://www.colkat.de>, 2017.11.06). Alternatively (if no taxonomic name could be found), a classification letter / number was assigned for a morphotype. The provided author name refers to the lowest practical taxonomic level (e.g. Hanula et al. 2009; Kutschbach-Brohl et al. 2010). Validation: name of scientific expert who checked the taxonomic determination. Management type of meadow in autumn: mown / unmown. Plant compartment: flower head, stem, tuft, leaves. All numbers represent total sums of all sample sites over the entire study period. Brown-labelled species names are thought to have hibernated in the soil. Green-labelled species names could only be found in flower heads and stems. Black-labelled species occurred in all plant compartments without any preference for a specific plant compartment.

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